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DDT transfer and metabolism in a forest litter macro-arthropod food chain[1])

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With 14 figures

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1. Introduction

Many investigations have been carried out on the abundance, persistence, disappearance and metabolism of DDT in the environment. Included among numerous papers showing that organisms are able to metabolize DDT is recent work at Michigan State University which indicates that soil-inhabiting Collembola (BUTCHER, KIRKNEL and ZABIK 1969), Acarina (AUCAMP and BUTCHER 1971) and microarthropods (KLEE, BUTCHER and ZABIK 1973) may play important roles in this phenomenon.

In light of these observations, it seemed worthwhile to look at the possibility that this phenomenon is common in other litter and soil arthropods. The project described here was designed to study the fate of DDT in a natural system once it became a part of the invertebrate food chain. The project, as related to the macro-arthropod (Insecta, Arachnida, Myriapods, Crustacea) predators, had two major goals. One was to study the ability of various cryptozoan fauna to degrade DDT in its different forms and to find out which degradation pathways were most important for each of the study animals. The second was to study the most important predators of the cryptozoan community and gain further insight into forest litter food chains.

2. Methods and materials

2.1. Collembola rearing and methods

The prime objective of this project was to study the effect of cryptozoan fauna on DDT rather than the effect of the pesticide on the arthropods. For this reason, a method had to be devised for introducing sublethal amounts of DDT into the food chain without contaminating the non-Collembola feeding forms directly. This was successfully accomplished by feeding the chemical to DDT-resistant Collembola (*Folsomia candida* WILLEM) prior to releasing them into the field plots. In addition to being highly resistant to DDT in all its forms, this species has a relatively short life cycle (about 21 days); is easy to rear; is able to adjust rapidly and can tolerate moving and handling.

The arthropod population of the study area was checked for background levels of DDT, DDE, and DDD prior to beginning the study. Since, DDT, DDE, and DDD were not detected in any arthropods tested at that time, an assumption was made that subsequent pesticide levels present in these animals were a result of the *Folsomia* introductions.

Collembola were reared in plastic boxes measuring $25 \times 35 \times 10$ centimeters. A liquid mixture of fifty percent plaster-of-paris and fifty percent charcoal was poured into the box to a depth of three to five centimeters. After this substrate hardened, Collembola were introduced and fed by sprinkling powdered brewer's yeast over the surface of the container two or three times a week. Collembola were reared at temperatures ranging between 21 and 26 °C.

1) Michigan Agricultural Experiment Station, Journal Article Number 7032

At the time of field release, Collembola were anesthetized with carbon dioxide and emptied into weighing containers. After weighing, they were moved to rearing containers and fed yeast containing 100,000 parts per million of the appropriate pesticide. This was accomplished by dissolving the DDT in acetone and adding the proper weight of yeast. The solution was mixed and allowed to stand overnight. The following day the acetone was evaporated and the yeast re-powdered. Yeast containing the pesticide was sprinkled over the entire surface of the container, and the Collembola were allowed to feed at 21 degrees centigrade for two days. Following this they were fed untreated yeast for two days and conditioned at 10 degrees centigrade for 24 hours. On the evening of the fourth day after feeding, the Collembola were sprinkled over the surface litter of the field plots at dusk.

Levels of DDT in the bodies of released Collembola generally ranged between 1,000 to 2,000 parts per million. On a per acre basis the actual rate of pesticide application was less than five grams per acre; very low when compared with standard field application levels.

2.2. Field plots

The site chosen for field studies in this investigation was a level, well-drained mesophytic beech and hard-maple forest situated near Michigan State University. The dominant canopy species of this type was beech *(Fagus grandifolia)*, hard maple *(Acer saccharum)*. Other species included the black cherry *(Prunus serotina)*, ironwood *(Ostrya virginiana)*, red oak *(Quercus rubra)*, and *Cornus florida*.

Study plots were five by five meters square. The plots were enclosed by a vertical strip of sheet metal, which was counter-sunk to a depth of four inches in the soil. Attached to the four-inch above-ground portion was a screen, which extended another eighteen inches vertically. The top of the enclosure was left open. The 22-inch (55.88 mm) high metal and screen fence was built in separate eight foot (2.44 m) sections which could easily be separated. This method of construction allowed the plots to be moved about in the woods for each new release. The interior of the enclosure was gridded into one-half meter squares with string so that samples could readily be selected at random.

Plots were established two to five days before sampling began. This period was intentionally kept short so that the enclosure effect would have as little influence as possible on the natural populations.

2.3. Sampling

Ten to twelve randomly selected sub-samples, 25×25 centimeters square, were taken from the 5×5 meter field plots at pre-selected times during the course of the study. A one-quarter meter wide strip immediately adjacent to the wall of the plot was left unsampled. Also left unsampled were two one-quarter meter walkway strips which intersected at right angles in the middle of each plot where a six inch (1524 mm) board was laid for access during sampling.

A relatively uniform sample was taken by pushing a sharp-edged metal 25×25 cm^2. frame into the leaf litter. A knife was used to cut around the inside of the frame, after which leaf and humus were scraped off to the mineral soil. The samples were placed in plastic bags and transferred to a styrofoam ice box for transporting back to the laboratory.

2.4. Sorting samples

Collections were hand sorted by placing each sample in a metal container with a one-half inch (127 mm) hardward cloth mesh bottom. After the larger animals were removed, the contents were shaken onto a white cloth where the remaining animals were collected immediately as they fell. Each animal was placed in a holding container until all samples were sorted. After sorting was completed, the arthropods were anesthetized with carbon dioxide for identification and weighing. After weighing, each group was placed in a vial and covered with 0.5 ml of hexane, macerated with a glass rod and quick-frozen until analysis could be completed with the gas chromatograph.

2.5. Analysis

Samples were analyzed on a Beckmann GC-4 gas chromatograph with a discharge electron capture detector. A 183 cm $\times$ 0.16 cm I. D. Pyrex column was packed with 11 % DC 200, 3 % QF-1 on 60/80 mesh Gas Chrom Q. Column temperature was 230 °C and detector temperature 310 °C. Helium flow through the column was 40 ml/min. Concentrations were calculated using peak height and were based on wet weights of all material analyzed. Standards were injected at the beginning of each run, after every ten to fifteen samples, and at the end of the run. Minimum detectable level for the instrument was 0.01 part per million for DDT and .003 parts per million for DDE. Minimum detectable levels in the arthropod tissue was 0.001 parts per million for DDT and 0.001 parts per million for DDE.

The DDT used was 99.9 % pure ESA reference standard grade, obtained from the U.S. Federal Pesticide Repository and from Geigy Chemical Company.

3. Results and discussion

3.1. Introduction

Forest litter arthropod predators were divided into four classes as follows: Araneida, Chilopoda, Coleoptera larva, and Coleoptera adults. For purposes of studying both the ability of various predators to metabolize DDT and the effects of various arthropods on the cryptozoan community, both taxonomic and weight class divisions were used. Weight classes were most important in studying predatory effects, and taxonomic determinations were of major importance in studying metabolism.

Collembola which were released into the field were fed either Op'-DDT, pp'-DDT or pp'-DDE.

Metabolic pathways used by the various forest arthropods were studied (Fig. 1).

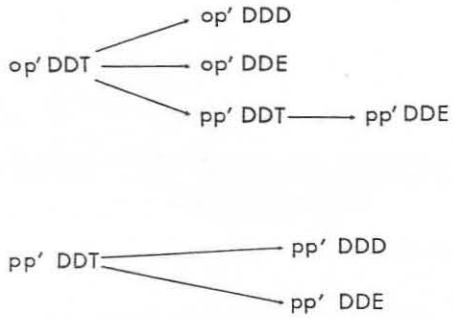

Fig. 1. Apparent degradation pathways of DDT metabolism in a forest invertebrate litter food chain.

3.2. Metabolism of pp'-DDT to pp'-DDE

Metabolism of pp'-DDT to pp'-DDE is the most important degradation pathway for cryptozoan predators when pp'-DDT is introduced into the food chain.

Differences in metabolism of pp'-DDT among the cryptozoan fauna are mostly a matter of degree. In animals which are fed on op'-DDT no pp'-DDE is present at the beginning (12 hours) of the same sequence (Fig. 2). The percent of arthropods fed on pp'-DDT which had measurable levels (above 0.01 ppm) of pp'-DDT and pp'-DDE after twelve hours reveals that DDE is present almost as often as is DDT; emphasizing the speed at which metabolism starts. Over a period of a few days, pp'-DDT is degraded beyond detectable levels (below 0.01 ppm) and the only remaining trace of the pesticide is pp'-DDE (Fig. 2).

The most rapid converters of pp'-DDT among the arthropod cryptozoan predators are Thomisidae (Fig. 3), Elateridae larva (Fig. 8), and Carabidae (Fig. 5). Upon first sampling twelve hours after release, most of the arthropods were only beginning to degrade the material, whereas the above forms contained only DDE in their systems.

Staphylinidae (Fig. 6) were also very rapid converters of pp'-DDT but showed some trace of DDT for the first six days after release; after which time they contained only DDE. These animals appear to have degraded most of the DDT after 12 hours. The ability to rapidly degrade DDT is most striking in the small beetles of this family.

A major group of predators is the spiders; which numerically may be the most striking degraderg among cryptozoan predators. Spiders were divided into three classes based on live weight as follows: small, medium, and large. For the purpose of metabolism studies, hahniids were not included with the small spiders; a group with which they would be classed on a weight basis. Hahniidae (Fig. 7), showed an above average ability to metabolize DDT; more closely related to that of the medium-sized spiders (Fig. 3). The small spiders (Fig. 7) showed the least (and most varied) ability to degrade the pesticide. This diversity may be explained by the fact that this was a group of heterogeneous forms, including several families and uncommon species which varied from sample to sample.

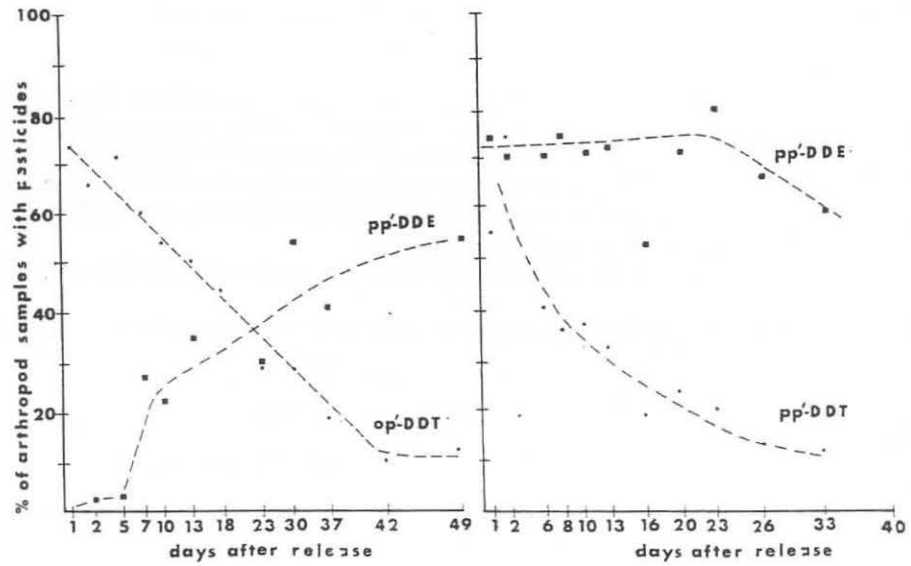

Fig. 2. Metabolism of DDT.

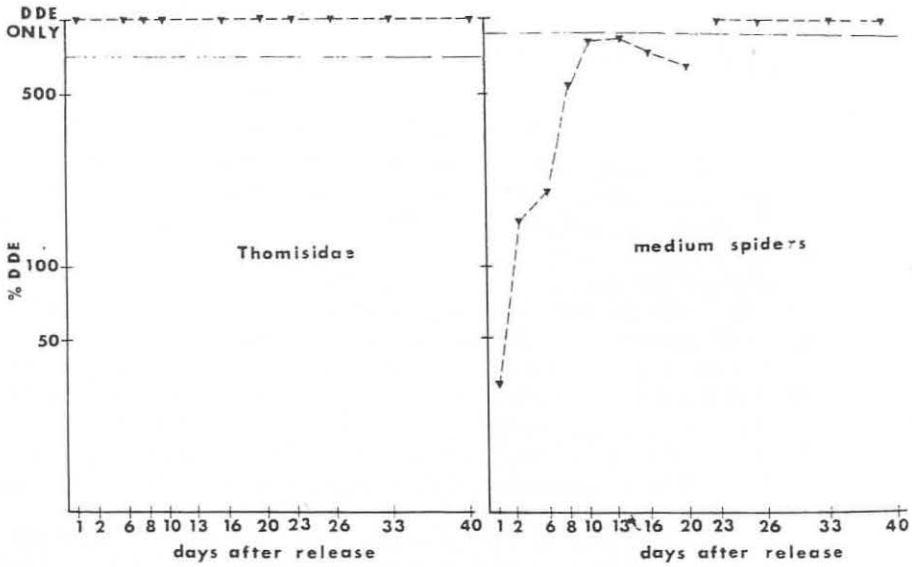

Fig. 3. Metabolism of Pp'-DDT to Pp'-DDE.

Outside of thomisids, the medium-sized class appears to be the best metabolizer of pp'-DDT among the Araneae. The date suggest they are efficient converters of pp'-DDT to pp'-DDE. After twenty-four to thirty-six hours, the amount of pp'-DDE is greater than the amount of pp'-DDT, but it is not until the eighth sample that the DDT drops under detectable levels.

Chilopoda (Fig. 4) were also found to metabolize pp'-DDT, but they appear to take longer than spiders to convert completely to DDE. Larger Chilopoda are significant degraders of pesticide in the community. The small forms (less than six months old) can be considered inefficient.

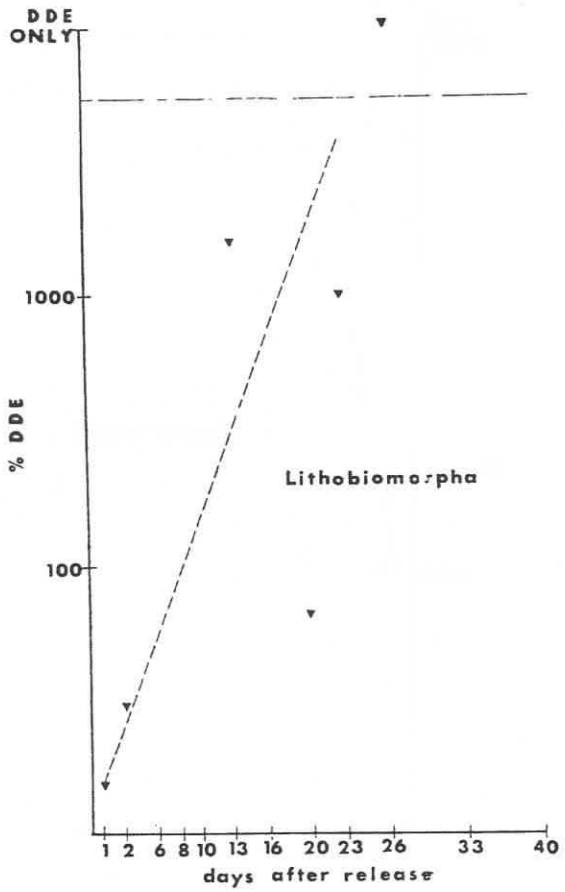

Fig. 4. Metabolism of Pp'-DDT to Pp'-DDE.

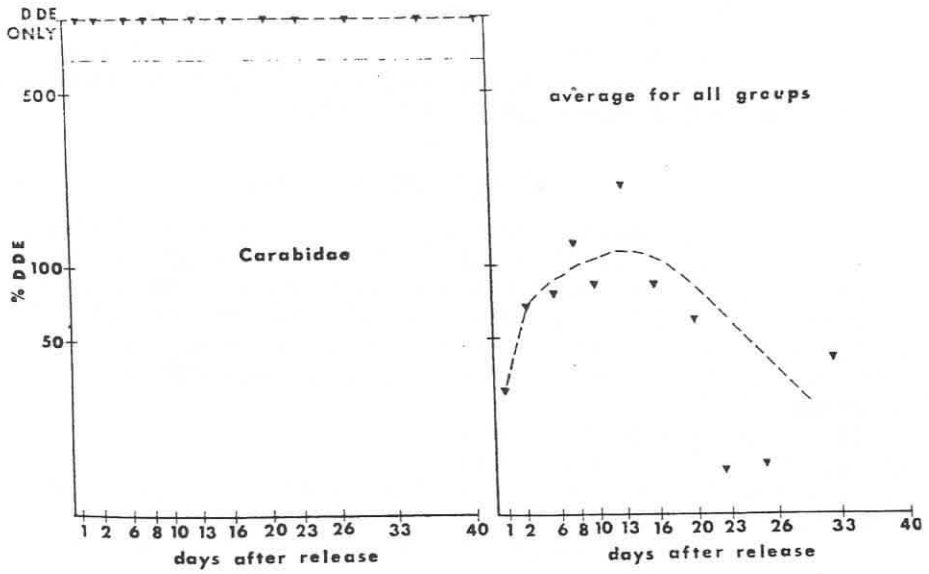

Fig. 5. Metabolism of Pp'-DDT to Pp'-DDE.

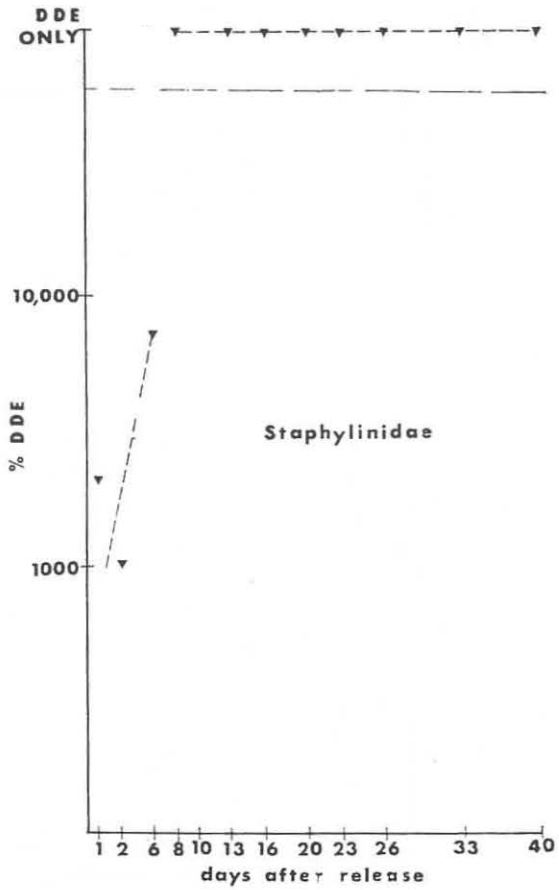

Fig. 6. Metabolism of Pp'-DDT to Pp'-DDE.

The average ratio of DDE to DDT for all arthropods (Fig. 5b) is considerably below that for the most efficient metabolizers. The average omits Staphylinidae figures because of the extremely high DDE conversion rate found in that group.

3.3. Op'-DDT metabolism

Op'-DDT is metabolized in several different directions. Given time however, a significant part of the op' compound will be metabolized to pp'-DDE through conversion to pp'-DDT and then to pp'-DDE (Fig. 8). Pp'-DDT is an important intermediate step in the breakdown of op'-DDT. Faunal differences in pathways of op'-DDT metabolism are for the most part a matter of degree with some groups forming more of one metabolic product than another. The data suggest that some groups of arthropods do not form certain metabolites; at least not in detectable levels.

Those cryptozoan predators studied which are capable of degrading op'-DDT can be divided into groups on the basis of the pathway which is most important; or on the basis of certain pathways not used. Since most arthropods studied form DDD at fairly consistent rates, it is discussed elsewhere.

On the basis of degradation pathways; cryptozoan predators can be divided into three major groups:

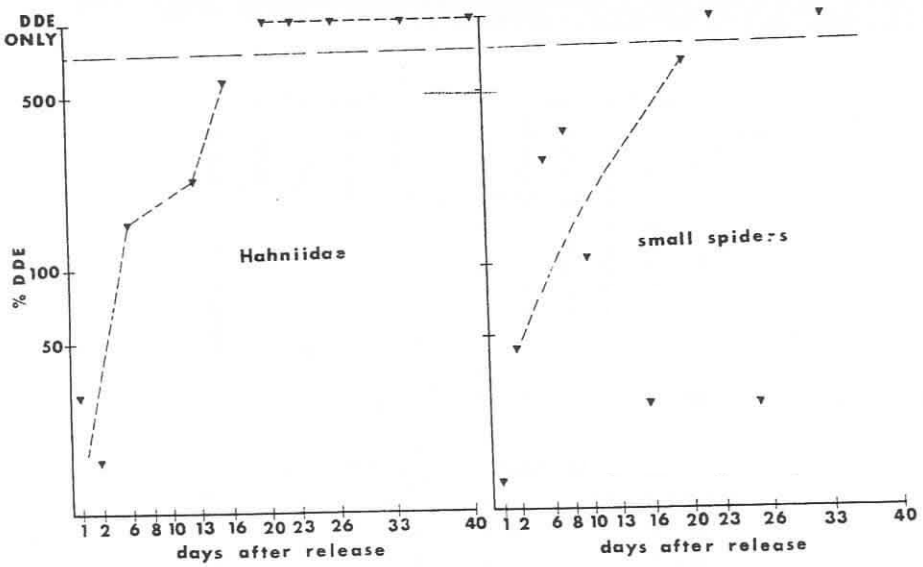

Fig. 7. Metabolism of Pp'-DDT to Pp'-DDE.

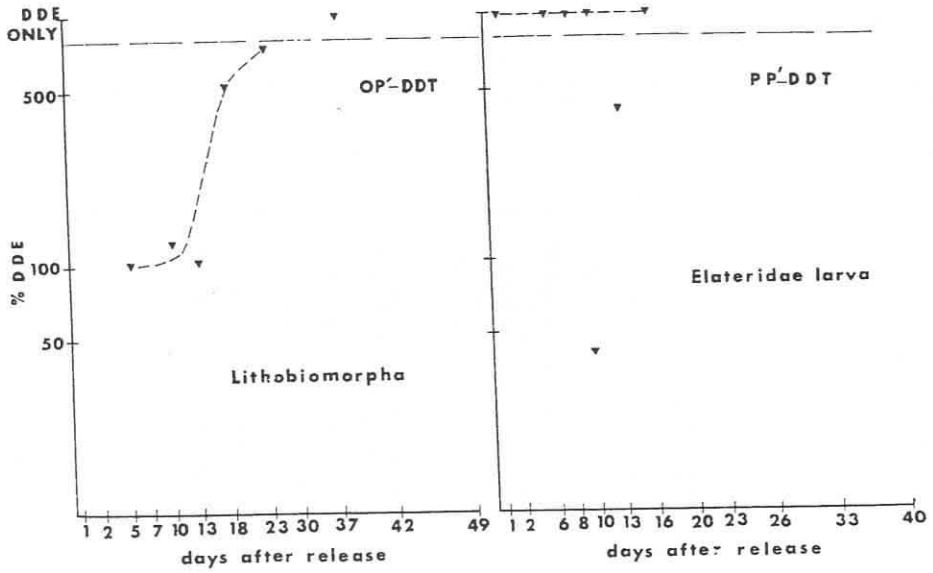

Fig. 8. Metabolism of DDT to Pp'-DDE.

Group I: Those which form op'-DDE. In this group, formation of op'-DDE starts almost immediately after feeding on op'-DDT-fed Collembola (Fig. 13b). Many of these arthropods also form pp'-DDT and then pp'-DDE, but this usually takes place at a slower rate than compared with other forms. The majority of spiders (Fig. 9a, 10b, 10d) fall into this group.

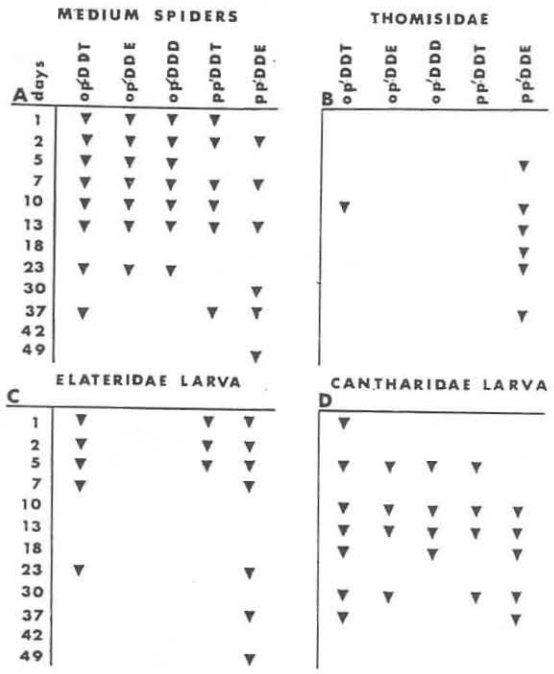

Fig. 9. Major routes of Op'-DDT metabolism.

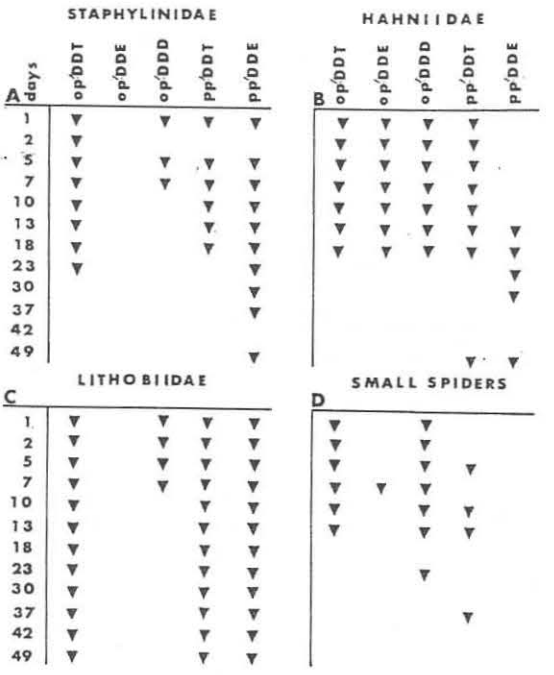

Fig. 10. Major routes of Op'-DDT metabolism.

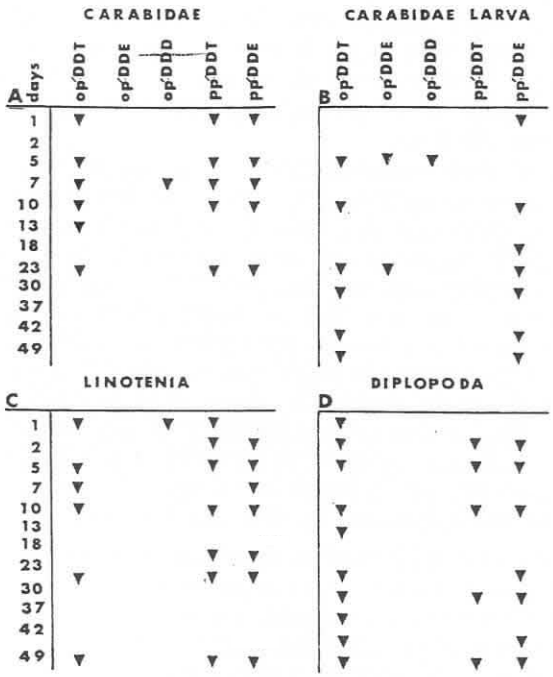

Fig. 11. Major routes of Op'-DDT metabolism.

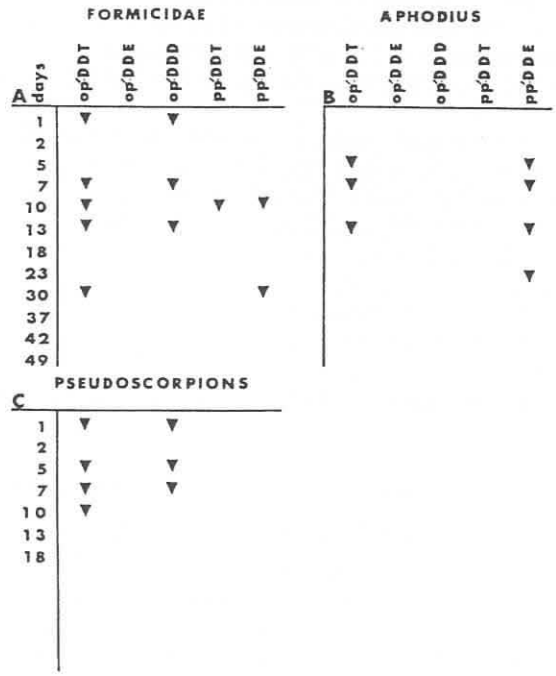

Fig. 12. Major routes of Op'-DDT metabolism.

Group II: Those which form no detectable levels of op′-DDE. All op′-DDT goes to pp′-DDT and then is converted to pp′-DDE. The rate of conversion is intermediate, and significant levels of pp′-DDT are found during most of the sample period. Also, small levels of op′-DDT remain during the sample period (Figure 10c). The major fauna in this group are the Chilopoda (Fig. 10c, 11c).

Group III: Some of the species in this group frequently lack pp′-DDT (Fig. 9b), and may show no pesticide except pp′-DDE (Fig. 12b); even after twelve hours. In many of them, larger amounts of pp′-DDE may also build up; and they usually do not accumulate very large levels of pp′-DDT. Indications are that all forms in this group degrade op′-DDT to pp′-DDT as an intermediate step, but that pp′-DDT in converted to pp′-DDE so rapidly, detectable levels are never reached. This reasoning is further supported by the extremely rapid rate at which some forms convert pp′-DDT to pp′-DDE when pp′-DDT is released in the field. Many of the arthropods which convert op′-DDT to pp′-DDE very rapidly are the same groups which are the most rapid converters of pp′-DDT to pp′-DDE, which may account for our inability to demonstrate pp′-DDT in some forms. Included in Group III are those forms which convert op′-DDT to pp′-DDT to pp′-DDE very rapidly (Fig. 10a). Many important predators are included in Group III, including Carabidae (Fig. 11a), Thomisidae (Fig. 9b), Staphylinidae (Fig. 10a), und Elateridae larva (Fig. 9c).

The amount of time required for various metabolites to reach detectable levels after release varies with the metabolite and the species involved. Pp′-DDE varied considerably between species but was the last product to appear, the last product to disappear, and frequently the only detectable trace of the DDT introduction left by the end of the sample period (Fig. 2). Pp′-DDE is the only material that constantly built up in the cryptozoan fauna during the entire study, whether the material fed was op′-DDT or pp′-DDT. All other metabolite levels peaked during the sample periods and then leveled off.

The amount of pp′-DDT in op′-DDT-fed arthropods varies as a percent of op′-DDT depending on the rate of degradation from op′-DDT to pp′-DDT and the ability to degrade pp′-DDT to pp′-DDE. Those macro-arthropod predators which are rapid degraders of pp′-DDT to pp′-DDE never accumulated large levels of pp′-DDT; while the slower metabolizing forms built up larger amounts of pp′-DDT and maintained high levels longer. For the most part, pp′-DDT reached maximum levels during the first half of the sample and then dropped off.

Among the macro-arthropod predators, conversion of op′-DDT to op′-DDE appeared to be primarily a spider phenomenon (Fig. 9a, 10b, 10d). Op′-DDE was most common in spiders but did not reach high levels. The only other arthropods found to contain op′-DDE were Cantharidae larvae (Fig. 9d) and Carabidae larvae (Figure 11b).

In general op′-DDE was detected early, and the level of op′-DDE increased as a percent of op′-DDT during the early part of the sample period; (Fig. 13b) and then dropped off. Ratios of op′-DDE to op′-DDT stayed small and did not build up to pp′-DDT fed levels. Average op′ levels did not exceed ten percent; but three to six percent are most common. Individual spiders contained op′-DDE levels which were up to thirty percent that of op′-DDT. Notable among these are spiders of the families Agelenidae and Hahniidae.

3.4. Op′-DDT metabolism of selected groups

As shown in Figure 9a, medium-sized spiders accounted for an important pathway in metabolism of op′-DDT through formation of op′-DDE. Op′-DDE was found to be common during the first half of the sample period and then it disappeared. All isomers found during the study were accounted for by the medium-sized psiders. Pp′-DDE was rare during the early samples (one spider has op′-DDE during the second sampling period) but increased in both quantity and frequently of occurrence during the study. Pp′-DDT was found in samples in significant amounts but was most common during the first half of the same period.

Thomisidae are very rapid converters of op'-DDT but are not typical of the majority of spiders in this respect. Pp'-DDE was the only isomer found during the early samples when most arthropod fauna (all other spiders) were just beginning to form pp'-DDE. Unlike other spiders, they did not appear to form op'-DDE. Three specimens of Thomisidae which did not conform to the above pattern of metabolism were smaller and may have been different species.

Elaterid larvae were rapid degraders of op'-DDT (Fig. 9c). In the early samples, op'-DDT, pp'-DDT, and pp'-DDE are present. Pp'-DDE soon became the major isomer and pp'-DDT was found only in the early samples. Among insect larvae analyzed, elaterids were the only group which did not show op'-DDE.

Cantharid larvae (Fig. 9d), at one time or another, yielded all isomers of op'-DDT. Pp'-DDE did not appear to reach detectable levels until about the fifth sample, but after that time it was found consistently. Op'-DDT appeared to remain throughout the sample period, as did most other isomers.

Staphylinidae (Fig. 10a) were rapid converters of op'-DDT. Pp'-DDE continued to increase during the study and it was the only isomer found after the eighth sample.

Hahniidae (Fig. 10b) exhibited a metabolism pattern very similar to medium-sized spiders. Pp'-DDE is not formed early but it is the only isomer that was detected in the later samples.

Lithobiidae (Fig. 10c) yielded both pp'-DDT and pp'-DDE immediately after release. Op'-DDT and pp'-DDT were observed during the entire sample period and relatively large levels of pp'-DDT were formed. Conversion to pp'-DDE appeared to occur at a slower rate.

Small-sized spiders (Fig. 10d) appeared to form smaller amounts of both op' and pp'-DDE than did larger spiders. Pp'-DDT was observed and pp'-DDE may have been present in small amounts. This was the most heterogeneous grouping of arthropods in the study, which accounts, in part, for the inconsistent results.

Carabid adults (Fig. 11a) did not form detectable levels of op'-DDE, but significant levels of pp'-DDT and pp'-DDE were noted shortly after release.

Carabid larvae (Fig. 11b), like cantharid larvae, yielded op'-DDE upon analysis. It is interesting that carabid larvae converted op'-DDT to op'-DDE but the adults did not. It would appear that the former have an ability to degrade pp'-DDT to pp'-DDE at a very rapid rate, since no pp'-DDT was found.

Linotenia (Geophilomorpha) (Fig. 11c) has a metabolism pattern very similar to the Lithobiomorpha, while Diplopoda (Fig. 11d) behaved similarly to related myriapodous arthropods.

Formicidae (Fig. 12a) appeared not to form op'-DDE, but exhibited the pp'-DDT to pp'-DDE route of op'-DDT metabolism.

Aphodius (Fig. 12b) was not collected consistently during the study, but results would indicate that they are good converters of op'-DDT. Pp'-DDE was formed immediately. This was the only isomer accounted for.

Pseudoscorpions (Fig. 12c) contained pesticide only in early samples and did not appear to form metabolites other than op'-DDD. The results appear not to be conclusive.

3.5. Metabolism of DDT to DDD

Previous work has shown that DDD is a metabolic product of a variety of microorganisms in the soil (Ko and Lockwood 1968). In studies of macroarthropod predators of the cryptozoan community reported here, data suggest that DDD is a product of gut micro-flora metabolism and DDE is a product of arthropod predator metabolism. This is assumed from the fact that metabolism of op'- and pp'-DDT to DDD is similar and consistent over a wide taxonomic range.

DDD in no cases approaches DDT levels in either percent concentration or parts per million levels. The percent level of DDD appears to increase slowly during the first half of

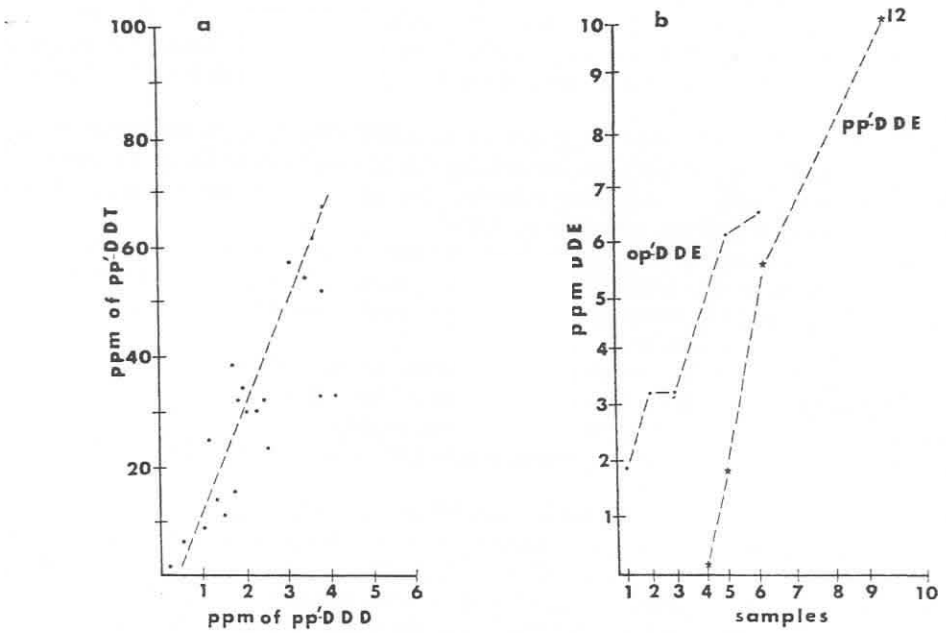

Fig. 13a. Relationship of Pp'-DDD in arthropods.
Fig. 13b. Formation of DDE by spiders fed Op'-DDT.

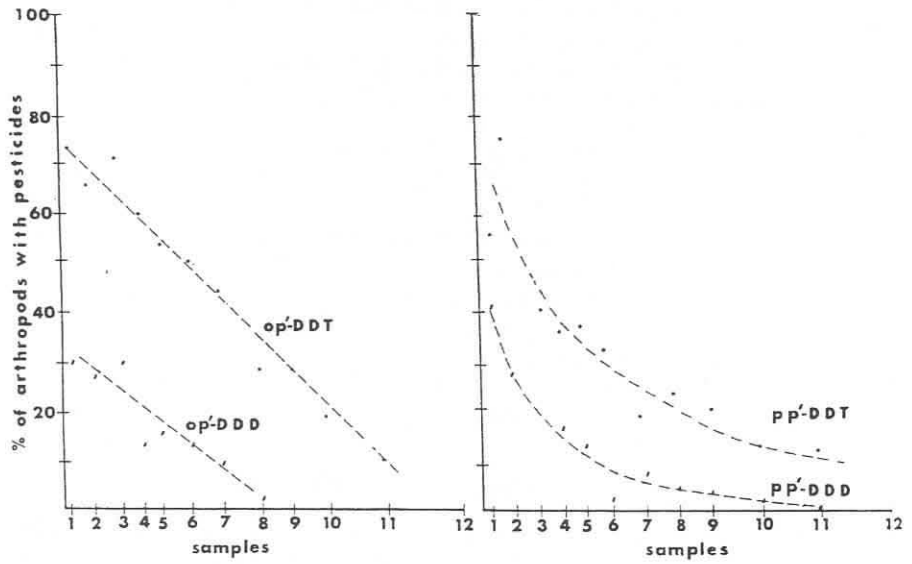

Fig. 14a, b. Disappearance of DDT and DDD.

the sample period and then drops off as DDT disappears from the system. DDD can generally be found to occur in all groups of animals at relatively low levels.

No group of arthropod predators studied accounted for more DDD than did any other group, but a direct relationship was noted between the amount of DDT and DDD. Animals with a high level of DDT also contained a high level of DDD (Fig. 13a). The percentage of

arthropods with DDT and DDD reveals that the occurrence of both in the macro-arthropods was very similar. In both op' and pp'-DDT introductions, DDT decreased at about the same rate as DDD (Fig. 14a, b). This is the reverse of the pattern noted for DDE. Also worth noting is that the actual DDD levels were highest during the first samples. This is particularly evident with respect to the pp'-DDT release, where DDT levels rapidly decreased through degradation to DDE.

The foregoing factors all suggest that DDD is a metabolic product of microflora in the gut of macro-cryptozoan predators and it is produced in proportion to the amount of DDT present.

3.6. Pp'-DDE introduction

3.6.0. *General remarks*

The introduction of Pp'-DDE into the food chain by means of Collembola was a convenient way to study predation of various groups in the plots. Weight class analysis proved to be most useful parameter.

When introduced into the food chain pp'-DDE was found to be the most stable of the materials used. Macro-cryptozoan predators appeared to accumulate large amounts of the material; much larger than was observed in the case of either DDT introductions. Some of the material was lost from the food chain during the study, but it still remained in significant amounts at the end of the sample period. No identifiable metabolites of DDE were found during the study. The major usefulness of its introduction was that it permitted study of predatory behaviour and efficiency within the community.

The movement of DDE in the food chain was very rapid and encompassing. Within a period of twelve hours, the pesticide was found in 95 % of the arthropods sampled.

The importance of an arthropod as a predator in this study was expressed in terms of Collembola eaten (Table 1), predator density, and wet biomass.

Estimates of Collembola eaten per animal and per sample period are listed in Table 1, based on one-half meter square samples. Estimates tend to be low due to losses by excretion and breakdown. Table 1 data assumes no food chain magnification.

Table 1. Estimate of number of labeled Collembola eaten, based upon concentrations of DDE retained by the predators

		Ave. No. of Predator animals captured per sample Period	Ave. No. of labeled Collembola eaten per animal	Estimated No. of labeled Collembola eaten per sample period	Percent of total labeled Collembola eaten by predators captured
Chilopoda large	A	.83	6.46	5.36	9.15
medium	B	1.50	6.88	10.32	17.63
small	C	3.30	.51	1.68	2.8
Spiders					
Hahniidae		3.00	1.70	5.10	8.71
Thomisidae		.83	1.05	.87	1.40
Agelenidae	A	1.10	6.07	6.67	13.10
	B	1.50	3.44	5.16	8.80
	C	1.30	1.17	1.52	2.59
Clubionidae	A	.30			
	B	1.50	3.89	5.83	10.00
Gnaphosidae		.30	.70	.21	0.35
Mixed small spiders		5.00	.94	4.70	8.00
Micryphantidae		3.00	.59	1.77	3.00
Staphylinidae		3.0	.50	1.50	2.56
Cantharidae larvae		.50	9.86	4.93	8.42
Insect larvae		1.83	1.60	2.92	4.98
Estimated total No. of labeled Collembola eaten by those predators captured				58.52	

The ability of an animal to degrade a compound involves many factors; some of which interact. Its ability to degrade the substance is important, but first the material must enter the arthropod. The effectiveness of predators as degraders depends not only on their ability to metabolize, but also on their efficiency as predators, their density, and their biomass in relation to the total community. In the case of pesticide breakdown, it may be important that the animal be consumed by a more efficient degrading species, particularly if the former is largely an accumulator, not a metabolizer of the compound. Certain species may not break the compound down rapidly enough. If these are susceptible to predation by vertebrates, the material can move out of the community into a community of other forms.

3.6.1. *Spiders as cryptozoan predators*

MOULDER (1970) considers spiders to be among the most important entomophagous predators in nature. Our study certainly indicates that they are among the most important of the forest floor fauna, in part due to their abundance. BORNEBUSCH (1930), VAN DER DRIFT (1951), TURNBULL (1960), GASDORF (1963), REICHLE and CROSSLEY (1967), and MOULDER (1970) have given estimates of forest spider populations.

Spiders consumed 55 % of the total Collembola accounted for in this study. Size class analysis revealed that small spiders had the greatest impact, accounting for 22.5 % of the total Collembola eaten by this group. Large spiders were least important of the three groups, accounting for 13.1 %; while medium-sized spiders were responsible for 20.1 % of the total. In this group, Hahniidae accounted for 38.7 % of the Collembola eaten, or two to three times as may Collembola per animal as the other small spiders, on the average. It is interesting that Collembola eaten per animal by the Hahniidae is more similar to that for the closely related small Agelenidae than it is to other small spiders. If Hahniidae were omitted from the "small" spider category, medium-sized spiders become the most important Collembola feeders.

Spiders are not dependent on smaller predators for the pesticide they ingest. Their prey includes small detritus-feeding mites, Collembola, larger Diptera larva, and even the largest invertebrates in the community. Spiders are exclusively predaceous, and are the most efficient in relation to prey and predator biomass. Many other forms are part-time predators, but they are also ominivorous and occur in many different trophic levels.

Generally, the larger forms of predators accounted for more Collembola per animal than did the smaller forms. In the Chilopoda, medium-sized specimens accounted for more Collembola than did the larger forms. This suggests that all size classes of Chilopoda feed directly on Collembola. On the other hand, spiders show a positive size relationship to Collembola consumed. This may be accounted for by larger spiders eating smaller predators instead of consuming Collembola directly.

Small-sized classes of predators consumed about the same number of Collembola per animal throughout the study, but larger forms consumed larger numbers of Collembola per animal with the passage of time. Larger forms also retained the pesticide longer. As compared with larger forms, smaller spiders showed much less variation in number of Collembola eaten per specimen and in parts per million DDE. This may indicate that the smaller forms eat Collembola directly and the larger forms obtain their pesticide from smaller predators.

Another indication that larger spider forms do not obtain their DDE level directly from Collembola may be inferred from the fact that medium-sized Agelenidae and medium-sized Clubionidae had the same levels, yet these two forms of spiders have different feeding habits. Agelenidae depend on a web and for the most part wait for food. The Clubionidae, on the other hand, move about in search of their food.

The present study indicates that spiders are the most important group of predators in the cryptozoan population. The have the largest biomass, largest density, and account for the largest number of Collembola equivalents consumed per arthropod of any of the macro-arthropods of the forest floor.

3.6.2. *Chilopoda as cryptozoan predators*

The Chilopoda are the second most important group of predators; accounting for 30 % of total Collembola eaten. Like the spiders, Chilopoda are conveniently separated into three classes based on size. The large-sized specimens are the adults of the population and are three years old or older. The medium-sized group contains the two-year-old specimens for the most part. The small chilopoda are young that have hatched during the spring of the current year.

The small specimens are most abundant and account for 0.51 Collembola per animal, or 2.8% of the total Collembola eaten. The medium-sized Chilopods accounted for 17 % of the Collembola eaten; which is about double that of the larger Chilopoda. When animals which accounted for the most Collembola per sample were analyzed, medium-sized Chilopoda were number one 57 % of the time. Chilopoda also accounted for the largest number of Collembola consumed by a single specimen (19.5).

In the study woodlot, Chilopoda of all size classes fed directly on Collembola. On a per animal basis, they are perhaps the most important Collembola predator. Laboratory studies have shown Chilopoda of all size classes to be efficient predators on Collembola.

3.6.3. *Coleoptera larvae as cryptozoan predators*

Coleoptera larvae were the only immature insects found to be of importance as crypto, zoan predators of released Collembola. Important Coleopte :a larvae consisted of Cantharidae, Staphylinidae, Carabidae, and Elateridae. Total Coleoptera larvae accounted for about 5 % of the Collembola eaten.

Cantharid larvae were found to be aggressive predators and on an "average per specimen" basis accounted for more Collembola than any other arthropod in the study area.

Carabid larvae were also aggressive predators and, along with the Elateridae, were very efficient degraders of the pesticide.

Staphylinid larvae were for the most part very small and sampling techniques employed were not adequate to make an assessment of their value.

3.6.4. *Coleoptera adults as cryptozoan predators*

Staphylinidae and Carabidae were the only adult beetles collected which may be of importance as predators. They were also the most common.

For the purpose of analysis, Staphylinidae were divided into two size classes: large and small. The small beetles were the most important of the two groups in terms of numerical abundance, total number of Collembola eaten, and number of Collembola eaten per animal. Small Staphylinidae accounted for 2.56 % of the total Collembola eaten.

4. Summary · Zusammenfassung · Résumé

Forest floor macro-arthropod cryptozoan fauna were found to be capable of degrading both op′ and pp′-DDT when these compounds were introduced directly into the food chain by means of DDT-resistant collembola that had been fed on the chemicals. The intermediate products of metabolism varied, depending on which isomer was used and which arthropod ingested the DDT; but the final products detected in both cases were pp′-DDE. The ability of all arthropods studied in this project to produce pp′-DDE, but not having the ability to further degrade the material could account for the presence of large concentrations of DDE in the upper levels of food chains. The presence of DDD appears to be explained by gut-microflora metabolism. Some groups of cryptozoan predators appeared to degrade by one pathway and not another, or they metabolized more rapidly by one pathway than did other groups. The metabolic pathways of DDT appear to be relatively consistent within the taxonomic groups of arthropods analyzed in this study.

Studies of important predators in the community revealed that spiders are the major cryptozoan predators of Collembola. Spiders were also found to be the most common predators of the macro-cryptozoan fauna.

The study provided information on the following: (1) characterization of the most important cryptozoan predators that feed on Collembola or Collembola predators; (2) an interpretation of the possible role of arthropods in degradation of DDT; (3) evidence that both op′-DDT and pp′-DDT can be degraded by arthropod systems; (4) metabolic conversion of DDT by cryptozoan predators in their natural environment; and (5) possible metabolic pathways of DDT degradation for a variety of forest arthropod predators.

DDT-Transfer und -Metabolismus in einer Nahrungskette von Waldstreu-Makro-Arthropoden

Die kryptozooische Makroarthropoden-Fauna im Waldboden zeigte die Fähigkeit, op′- und pp′-DDT abzubauen, wenn mit diesen Produkten gefütterte Collembolen direkt in die Nahrungskette eingeführt wurden. Die Zwischenprodukte in der Abbaufolge variierten jeweils in Abhängigkeit von dem verwendeten Isomer und der Arthropoden-Art, die das DDT aufnahm. In allen Fällen war pp′-DDE das Endprodukt. Die Fähigkeit aller in diesem Projekt untersuchten Arthropoden, pp′-DDE zu produzieren, nicht aber den Stoff weiter abzubauen, mag für das Vorhandensein hoher Konzentrationen von DDE in den oberen Stufen der Nahrungskette verantwortlich sein. Vorhandenes DDD scheint auf den Darmflora-Metabolismus zurückzuführen zu sein. Manche Gruppen kryptozoischer Räuber schienen nur über einen bestimmten Weg abzubauen, andererseits war die Geschwindigkeit des Abbaus über denselben Weg von Gruppe zu Gruppe verschieden. Die Abbauwege von DDT erscheinen innerhalb der einzelnen Gruppen von Arthropoden, die in dieser Arbeit analysiert wurden, verhältnismäßig beständig.

Studien an wichtigen Räubern in der Population zeigten, daß Spinnen die wesentlichen kryptozoischen Räuber waren, gemessen am Fraß von Collembolen. Außerdem traten sie als die häufigsten Prädatoren der kryptozoischen Makrofauna hervor.

Die Arbeit brachte Information in folgenden Punkten: (1) Charakterisierung der wichtigsten kryptozoischen Prädatoren, die sich von Collembolen oder Collembolen-Räubern nähren; (2) Interpretation der möglichen Rolle von Arthropoden im Abbau von DDT; (3) Beweis, daß sowohl op′-DDT als auch pp′-DDT in Arthropoden-Systemen abgebaut werden können; (4) Abbau von DDT durch kryptozoische Räuber in ihrer natürlichen Umwelt; und (5) mögliche Wege des Abbaues von DDT in einer Reihe von räuberischen Arthropoden des Waldbodens.

Transfert et métabolisme du DDT dans une chaîne trophique de Macroarthropodes en litière forestière

Les Macro-arthropodes cryptozoïques du sol forestier ont montré la faculté de dégrader les deux isomères du DDT, op′-DDT et pp′-DDT. Leur introduction directe dans la chaîne alimentaire a été réalisée à l'aide de Collemboles résistants qui ont été nourris de ces substances. Différents produits métaboliques intermédiaires sont obtenus: ils dépendent de la nature de l'isomère utilisé et du type d'Arthropode qui l'ingère. Cependant le produit final est dans les deux cas le pp′-DDE. Tous les Arthropodes étudiés montrent cette faculté de produire du pp′-DDE, mais ils sont incapables de poursuivre la dégradation au-delà. Ceci permet d'expliquer les concentrations élevées de DDE présentes aux niveaux supérieurs des chaînes alimentaires. La présence de DDD semble être liée au métabolisme de la microflore intestinale. Certains groupes de prédateurs semblent dégrader par une seule voie de préférence à une autre ou bien le métabolisme par une voie est plus rapide chez eux que chez les autres groupes. Les voies métaboliques du DDT paraissent relativement similaires au sein des groupes taxonomiques d'Arthropodes analysés.

L'étude de l'importance des prédateurs dans la communauté a révélé que les araignées sont les principaux prédateurs cryptozoïques tant des Collemboles que de la faune macro-cryptozoïque.

L'étude a permis (1) de caractériser les prédateurs cryptozoïques les plus importants qui se nourrissent des Collemboles et de prédateurs de Collemboles; (2) de donner une interprétation du rôle possible des Arthropodes dans la dégradation du DDT; (3) de mettre en évidence la dégradation de ses deux isomères par les Arthropodes, (4) la conversion métabolique du DDT par les prédateurs dans leur habitat naturel et (5) les voies métaboliques possibles de la dégradation du DDT par divers Arthropodes forestiers prédateurs.

5.0. Selected literature

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